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# A new *Entheus* (Hesperiidae: Eudaminae) from Colombia and Panama is most distinctive in the *E. gentius* group

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**Abstract.** A new species of *Entheus* is described from the Magdalena Valley in Colombia (type locality) and Panama. *E. huertasae*, **sp. nov.** stands out from other species in the *E. gentius* group by the black posterior half on ventral hindwing, the placement of spots in the apical yellow band on the forewing, width of hindwing black margin, mostly yellow anal fold, characters of the male genitalia, such as penis shape and length of tegumen processes, and about 7% difference in DNA barcode sequence. Identification key to males in the *E. gentius* group is given, and difficulties with *Entheus* taxonomy are discussed.

**Resumen.** Se describe una nueva especie de *Entheus* habitante del Valle del río Magdalena en Colombia (localidad tipo) y Panamá. *E. huertasae*, **sp. nov.** se distingue de las otras especies del grupo *E. gentius* por tener la mitad posterior negra en las alas posteriores ventrales, por la disposición de puntos en la banda amarilla apical de las alas anteriores, por el ancho del margen negro de las alas posteriores, por el pliegue anal que, en su mayor parte, es amarillo, por las características de los genitales masculinos como la forma del pene y la longitud de los procesos de tegumen, y la diferencia de aproximadamente el 7% en la secuencia de código de barras de ADN. Se presenta una clave para identificar los machos del grupo *E. gentius*, y se analizan algunas dificultades en la taxonomía de especies de *Entheus*.

**Key words:** new species, taxonomy, Neotropical, skipper butterfly, cryptic species, field marks, COI, mitochondrial DNA.

## Introduction

The genus *Entheus* Hübner, [1819] includes over a dozen showy skipper species visually characterized by a contrasting combination of black, white, yellow and orange colors (Warren *et al.*, 2013). Its comprehensive synonymy and bibliography are provided by Mielke (2005), species groups are discussed by Grishin (2012) and all recognized taxa and many extant primary types are illustrated in Warren *et al.* (2013). *Entheus* is notorious for extreme sexual dimorphism that renders confident sex association by appearance nearly impossible; and for taxonomic hardship caused by the loss of primary types for several difficult to recognize taxa, presence of many cryptic species, and curious for many Hesperiidae: Eudaminae similarity of male genitalia even in very distantly related species (Evans, 1952; Steinhauser, 1989; Austin *et al.*, 1997; Austin, 1997; Janzen *et al.*, 2011; Grishin, 2012). Interestingly, *Entheus* female genitalia offer an array of diagnostic characters and are frequently more distinct than male genitalia (Austin *et al.*, 1997; Steinhauser, 1989), but their potential power in *Entheus* taxonomy is yet to be realized, partly due to the difficulties with sex associations. Adults are secretive, routinely perching concealed on lower leaf surfaces in shady wooded areas (similarly to many Riodinidae), and many species are very rare in collections, exacerbating taxonomic puzzles.

The first glimpse into the hidden diversity of cryptic species in *Entheus* was given by Steinhauser, Austin and Mielke (Steinhauser, 1989; Austin *et al.*, 1997; Austin, 1997). Spectacular work by Janzen and colleagues in rearing of many dozens of *Entheus* specimens from caterpillars collected in the wild in the Area de Conservación Guanacaste (northwestern

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Costa Rica), followed by careful analysis of their foodplants, wing patterns, genitalia and mitochondrial DNA COI barcode snippets, re-iterated this notion (Janzen *et al.*, 2011). For instance, Janzen *et al.* (2011) reported and illustrated three likely undescribed *Entheus* species from the *E. matho* Godman & Salvin, 1879 group. These three species are close to each other in facies and are very similar in genitalia, yet they differ significantly in larval food plants and ecology. Their DNA barcodes are also slightly but consistently divergent. Thus, they likely represent distinct sympatric species and exemplify cryptic species diversity in *Entheus* that has also been revealed through traditional taxonomic methods (Austin *et al.*, 1997; Austin, 1997). The three cryptic *E. matho* group putative species, presently termed "Burns01", "Burns02", and "Burns03", offer valuable clues about phenotypic differences in *Entheus* that may be indicative of species-status versus individual variation, and provide definitive male-female associations in taxa displaying marked sexual dimorphism.

While it might seem imprudent to approach *Entheus* taxonomy in any way short of a comprehensive revision fully addressing the name-bearing types to define the identities of existing names, it is also important to characterize the biodiversity and name newly discovered species in timely fashion. Such an approach to the problem (one bit at a time) has been taking place (Austin *et al.*, 1997; Austin, 1997; Grishin, 2012). Due to the scarcity of many *Entheus* species, some of these were described from a single specimen. While this tactic has a higher risk in coining an unnecessary synonym and certain potential for creating future taxonomic problems, it attracts researchers and butterfly enthusiasts to these unique phenotypes with all likelihood representing distinct biological species and facilitates further studies. This, when done with due diligence, should be preferred to placing an unusual specimen in "taxonomic limbo" for years with hopes to obtain a series at some later point. For instance, after I named *E. warreni* Grishin 2012 from a single specimen, Ernst Brockmann (pers. comm.), prompted by the description, found another *E. warreni* specimen (illustrated in Warren *et al.*, 2013), which otherwise might have remained unnoticed (i.e. simply dismissed as "*E. matho*") for years to come. Moreover, this specimen has been barcoded by the BOLD project (Ratnasingham & Hebert, 2007), and further analysis of this distinctive species in now possible, including a segment of its DNA sequence.

Here, I build on the work of Austin *et al.* (1997), who clarified the identity of *E. gentius* (Cramer, 1777) by designating a neotype and described two new species similar to *E. gentius* in appearance: *E. bombus* Austin, Mielke & Steinhauser, 1997 and *E. aureolus* Austin, Mielke & Steinhauser, 1997. These three species comprise the *E. gentius* group. I describe a fourth species, characterized by unique wing patterns and genitalia features that represent a mixture of characters of the three named species, and discuss similarity and variation in *Entheus* and its relevance for delineation of *Entheus* taxa in light of available DNA barcode data. Possibly due to extreme sexual dimorphism, I was not able to find and associate any females with the males of this new species, therefore females are not discussed in this study.

## Materials and methods

*Entheus* specimens were examined in the following collections: American Museum of Natural History, New York, NY (AMNH); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); Natural History Museum, London, UK (BMNH); Museum für Naturkunde, Berlin, Germany (ZMHB); McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL (MGCL); Carnegie Museum of Natural History, Pittsburgh, PA (CMNH); Academy of Natural Sciences Philadelphia Collection, Philadelphia, PA (ANSP); Senckenberg Museum für Tierkunde, Dresden, Germany (MTD); Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (DEI); and Texas A&M University Insect Collection, College Station, TX (TAMU). Photographs by Ernst Brockmann of primary types in the Universidade Federal do Paraná, Curitiba, Brazil (DZUP) collection were also examined. Standard entomological techniques were used for dissection (Robbins, 1991), i.e. distal part of adult abdomen was broken off, soaked for 40 minutes (or until ready) in 10% KOH at 60°C, dissected and subsequently stored in a small glycerol-filled vial on the pin under the specimen. Genitalia and wing venation terminology follows Steinhauser (1981) with modifications. Length measurements are in metric units and were made from photographs of specimens taken with a scale and magnified on a computer screen. Photographs of specimens and dry genitalia were taken by the author with a Nikon D800 camera through a 105 mm f/2.8G AF-S VR Micro-Nikkor lens; dissected genitalia were photographed in glycerol with Nikon D200 camera without lens through microscopes at 4x, 5x, and 6.4x magnifications. Images were assembled and edited in Photoshop CS5.1. Genitalic photographs were taken in several focus slices and stacked in Photoshop to increase depth of field.

DNA was extracted and isolated using Macherey-Nagel (MN) NucleoSpin® tissue kit following the

manufacturer's protocol. An abdomen (intact, and used for genitalia dissection after DNA extraction) or a single leg (cut by scissors into small pieces) were lysed in 90 µl MN T1 buffer with 12 µl MN Proteinase K (22 mg/ml) by overnight incubation at 56°C. DNA was eluted to the final volume of 120 µl (DNA concentration varied from 0.03 to 0.4 ng/µl). Barcode region was PCR-amplified in two segments (307, 408 bp) using the following sets of primers: LepF (forward, 5'-ATTCAACCAATCATAAAGATATTGG-3') – MLepR (reverse, 5'-CCTGTTCCAGCTCCATTTTC-3') and MLepF (forward, 5'-GCTTTCCCACGAATAAATAATA-3') – LepR (reverse, 5'-TAAACTTCTGGATGTCCAAAAAATCA-3'). Each PCR reaction contained 8.4 µl of DNA template (for concentrations below 0.4 ng/µl, or volume needed to supply approximately 3 ng of DNA plus molecular biology grade water up to 8.4 µl), 0.8 µl of each primer (12.5 µM) and 10 µl Invitrogen AmpliTaq Gold 360 master mix. PCR products were cleaned using MN NucleoSpin® Gel and PCR Clean-up kit and eluted to the final volume 20 µl. PCR products were sequenced from either MLepR (for the 307 bp segment) or MLepF (for the 408 bp segment) primers using Applied Biosystems Inc. (ABI) Big Dye Terminator 3.1 kit on ABI capillary instrument in the DNA Sequencing Core Facility of the McDermott Center at UT Southwestern. Sequence trace files were visualized in FinchTV and full barcode was manually assembled from the two segments in a text editor.

Additional DNA sequences were downloaded from GenBank (http://genbank.gov), aligned by hand since they matched throughout the length without insertions or deletions, and analyzed using the Phylogeny.fr server (http://www.phylogeny.fr) with default parameters (Dereeper *et al.*, 2008). Many of these sequences have been reported in Janzen *et al.* (2011) and photos of specimens are available from the Area de Conservación Guanacaste (ACG) on-line database (Janzen & Hallwachs, 2013) and BOLD database (Ratnasingham & Hebert, 2007) to confirm or suggest identification.

## Results

Selecting specimens for photography in the AMNH collection, among *E. gentius*-group males I noticed an *Entheus*, mounted ventral side up, with a broadly black instead of yellow-orange posterior hindwing, a character not observed in other species of the group. This specimen also appeared slightly larger than a typical male. A more careful inspection revealed other unique aspects and prompted a genitalic dissection. Comparison with the named *Entheus* species and analysis of their variation and diagnostic traits suggested that this specimen belongs to an undescribed species, which appears to be more distinct from others in the *E. gentius* group. This new species is named here.

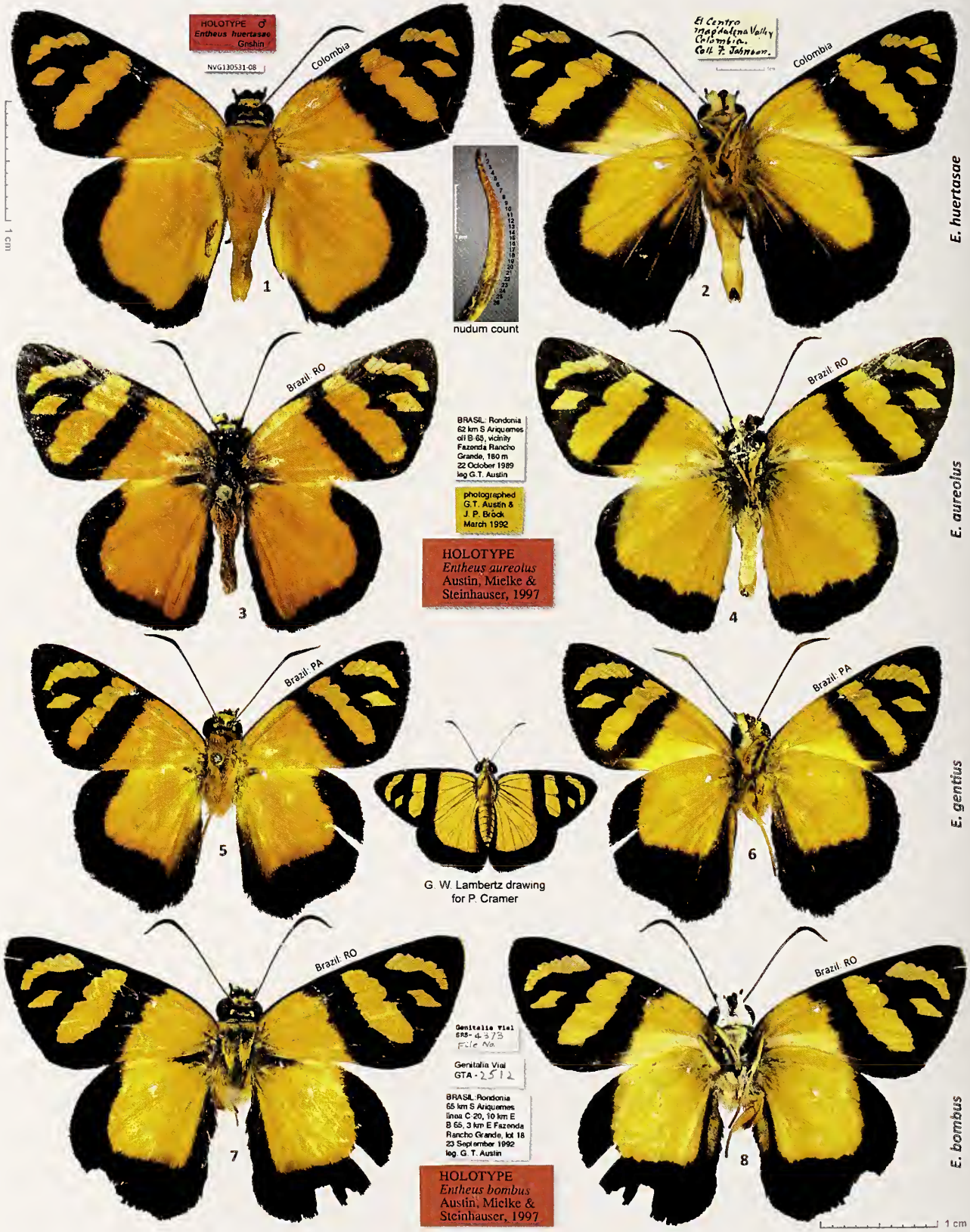
### *Entheus huertasae* Grishin, new species

(Figs. 1–2, 9–26, 27a, 28 part, 29 part)

**Description.** *Male* (Figs. 1–2 & 9–24): right forewing length = 20 mm in holotype (for all ten type series specimens mean = 20 mm, standard deviation = 1 mm, range = 18.5–21 mm). ***Forewing*** elongated, triangular, apex pointed, not produced, outer margin convex, straighter near the tornus. ***Dorsal forewing*** black marked with yellow-orange: yellow-orange basal third; yellow-orange discal band from vein Sc to the middle of $CuA_2$-2A cell, edges irregular, almost parallel, band constricted along the cubitus; rhomboidal orange-yellow spot in cell $M_3$-$CuA_1$ closer to outer margin than to the base of the cell, spot separated from the discal band; six conjoined subapical spots between $R_2$ and $M_3$, spots separated from the discal band, three spots closer to costa hyaline (the only hyaline areas on wings) and in most specimens offset basad along $R_5$ relative to the other three spots. ***Ventral forewing*** pattern similar to dorsal, yellow-orange areas paler especially in $CuA_2$-2A and 2A cells; 2A cell pale-yellow except distal quarter. ***Hindwing*** slightly angled at $M_3$, with a hint of anal lobe at 2A. ***Dorsal hindwing*** yellow-orange with a black margin narrowing from covering distal third of cells near apex to the width of anal fold at tornus; basal half of anal fold yellow-orange in most specimens, slightly paler than the wing ground color, but overscaled black almost from the base in some specimens. ***Ventral hindwing*** yellow-orange with the black margin broader than on the dorsal side widening from between veins $M_2$ and $M_3$ to tornus; hindwing black in posterior half posteriad $CuA_1$ with some yellow-orange overscaling at the bases of cells (especially in $CuA_2$-2A) and the base of anal fold. ***Fringes*** black, the same color as wing margins. ***Head*** yellow-orange above, two small black spots between the eyes near palpi, two large conjoined black spots between antennae and a black narrow band between the eyes, eyes dark-grayish-brown, framed with black scales; collar yellow-orange with a posterior belt of black scales; palpi black above, pale-cream below, last segment black with some yellow scales below; antenna black with yellow scales below mostly near and along the club, nudum of the right antenna of the holotype of 26 segments (nudum of 25, 26, 26, 26 and 27 segments in five paratypes). ***Thorax and abdomen*** yellow-orange above, thorax yellow-orange below with areas of black scales near the legs, abdomen pale yellow below; legs yellow-orange, hind tibial tufts (best seen in Fig. 12) with inner portion yellow-brownish, extending distad to near 3/4 length of first tarsomere, outer portion pale-brown with darker, brown tip (1/4 to 1/2 outer portion length) and short, extending distad 1/3 to 1/2 length of first tarsomere.

***Male genitalia*** (Figs. 26 and 27a): typical for the group, tegumen narrower in lateral view than in other species from the *E. gentius* group, with two long and slender caudal processes that nearly reach the distal end of uncus; uncus longer than in *E. aureolus*, dorsally straight in lateral view with a caudal notch, uncus arms narrower and longer than those of *E. gentius* and *E. bombus*, more similar to those in *E. aureolus*; valva narrower than in other species from *E. gentius* group, costal process of valva reaches into the harpe; aedeagus narrower and less bulbous that in *E. gentius* and *E. bombus*, with longer phallobase, most similar to that of *E. aureolus*, with 10 spike-like cornuti in the holotype: 1 very long, 2 long and 3 slightly shorter than others. The exact number of cornuti is variable (as in other species) and is 13 in one paratype.

***Female:*** unknown or unrecognized.


HOLOTYPE ♂
Entheus huertasae
Grishin
NVG130531-08
Colombia
1
El Centro
Magdalena Valley
Colombia.
Coll. F. Johnson.
Colombia
2
E. huertasae
nudum count
Brazil: RO
3
BRASIL: Rondonia
62 km S Ariquemes
off B-65, vicinity
Fazenda Rancho
Grande, 180 m
22 October 1989
leg G.T. Austin
photographed
G.T. Austin &
J. P. Bröck
March 1992
HOLOTYPE
Entheus aureolus
Austin, Mielke &
Steinhauser, 1997
Brazil: RO
4
E. aureolus
Brazil: PA
5
Brazil: PA
6
E. gentius
G. W. Lambertz drawing
for P. Cramer
Brazil: RO
7
Genitalia Vial
SRS-4373
File No.
Genitalia Vial
GTA-2512
BRASIL: Rondonia
65 km S Ariquemes
linea C-20, 10 km E
B 65, 3 km E Fazenda
Rancho Grande, lot 18
23 September 1992
leg. G. T. Austin
HOLOTYPE
Entheus bombus
Austin, Mielke &
Steinhauser, 1997
Brazil: RO
8
E. bombus
1 cm
1 cm

**Types.** Holotype male, mounted ventral side up, with the following labels: white, handwritten in black ink: / El Centro / Magdalena Valley / Colombia. / Coll. F. Johnson. /; white, printed: / NVG130531-08 /; red, printed: / HOLOTYPE ♂ / *Entheus huertasae* / Grishin /. A vial with genitalia is pinned under the specimen above the labels. The holotype is in the collection of the American Museum of Natural History, New York, NY (AMNH). Nine paratypes, all males from Panama: one from Colón Prov., Rio Guanche, 17-Jan-1976, leg. G. B. Small, specimen number OM. 45.496; five from Panamá Prov.: Distrito de El Llano, Cordillera de San Blas, north of El Llano, ca. 330 m, (three of these specimens have "5mi N El Llano" and "9° 17'N 79° 00'W" on the labels), 19-May- and {5, 6, 8, 14}-Jun-1978, leg. G. B. Small (DNA extraction codes are NVG-1759, NVG-1782 and NVG-1784 for those collected on 19-May, 8-Jun and 6-Jun, respectively); one from Panamá Prov., Cerro Jefe, 490 m, 24-Sep-1973, leg. G. B. Small, DNA extraction NVG-1784; one from Veraguas Prov., near Punta Mariato, 800 m, 7° 13'N 80° 53'W, 12-Feb-1982, leg G. B. Small; and one from Darién Prov., Darién National Park, Rancho Frio, 08° 01' 11.3"N 77° 43' 57.0"W, 100 m, 22-Jul-2013, leg. A. Thurman. The paratype from Colón Prov. is in the research collection of Olaf H. H. Mielke (Curitiba, Brazil) and the paratype from Darien Prov. is in the research collection of Albert Thurman (Phoenix, Arizona, USA), all other paratypes are in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

**Type locality.** Colombia: Santander department, Magdalena River Valley, 18 air km southeast of Barrancabermeja, El Centro, GPS coordinates about 6° 56'N 73° 45'W, elevation 100-150 m.

**DNA barcode sequences.** Paratype from Panama: Panamá Prov., Distrito de El Llano, Cordillera de San Blas, N of El Llano, 330 m, 19-May-1978, leg. G. B. Small, genitalia vial No. NVG131129-01, DNA extraction NVG-1759 (Figs. 9–10), GenBank Accession KF921081, 658 base pairs:

AACCTTATATTTTATTTTTGGAATTTGAGCAGGAATGGTAGGTACT
TCTTTAAGATTACTAATTCGAACTGAATTAGGAACTCCAGGAT
CATTAATTGGCGATGATCAAATTTATAATACTATTGTAACTGCA
CATGCTTTTATCATAATTTTTTTTATAGTTATGCCAATTATAATT
GGCGGATTTGGAAATTGATTAGTTCCTTTAATATTGGGAGCTC
CCGATATAGCTTTCCCTCGTATAAATAATATAAGTTTTTGACTTT
TACCCCCATCATTAACATTATTAATCTCAAGAAGAATTGTTG
AAAATGGGGCCGGAACAGGATGAACTGTTTATCCCCCATTATCTG
CTAATATCGCACATCAAGGTTCTTCAGTAGATTTAGCAATTTTTTCC
CTACATTTAGCTGGAATTTCATCTATTTTAGGAGCTATTAATTTT
ATTACAACAATTATTAATATGCGAATTAGAAATTTATCTTTTGATC
AAATACCTTTATTCGTTTGAGCTGTAGGTATTACTGCTTTACTTTT
ATTATTATCTTTACCTGTATTAGCTGGAGCTATTACTATATTATT
AACTGATCGAAATTTAAATACATCATTTTTTGATCCTGCTGGAGGAGG
AGATCCAATTCTTTACCAACATTTATTT

Partial barcodes were obtained for three more paratypes: NVG-1782, NVG-1783 and NVG-1784 and deposited in GenBank with accessions KF921082, KF921083 and KF921084, respectively. Two of these were identical in sequence to the full NVG-1759 barcode shown above, and NVG-1783 revealed 2 bp difference from it: position 100 T (not C) and position 181 T (not C), numbering from 1 to 658 for NVG-1759 sequence.

**Etymology.** It is my pleasure to name this new species in honor of Blanca Huertas, Curator of Lepidoptera, Natural History Museum, London, UK. Blanca's help has been instrumental in many projects dealing with Neotropical butterflies and skippers. Her diligence and hard work in helping researchers across the world, bit-by-bit, day after day has built up an admirable legacy. She is from Colombia and has a radiant, sunny and warm personality, a keen sense for recognizing talent, passion for butterflies and working with people, and a constant drive for excellence and accomplishing challenging projects. This beautiful, beamy and bright yellow-orange *Entheus* species, standing out due to its unique appearance, is also from Colombia and reminded me of her. The name is a feminine noun in the genitive case.

**Distribution.** The species is currently known from Panama (Colón, Panamá, Veraguas and Darién Provinces) and Colombia (Magdalena Valley) (Fig. 25) and has been recorded from forested areas at various low to mid-range elevations (100 to 800 m).

**Diagnosis.** The new species belongs to *Entheus* because it possesses the following characters used by Evans (1952) to circumscribe the genus: **A)** the third segment of palpi is stout and spatulate, positioned close to the outer edge of the second segment; **B)** antennae are bent at the beginning of nudum (i.e. segments with scaleless areas on antennal club), not distad of the beginning; **C)** forewing vein $M_3$ origin is in the middle between veins $M_2$ and $CuA_1$, not twice as far from vein $CuA_1$ than from vein $M_2$; and **D)** it lacks a costal fold.

The new species belongs to the *E. gentius* group because: **a)** it has tuft of long scales on hind tibia (Fig. 2 & 9–24); **b)** its valva is with a long and slender costal process (Fig. 26); **c)** forewing spots and bands are yellow and not white; **d)** hindwing is largely yellow-orange and not entirely black or dark brown; and **e)** forewing is with a large rhomboidal spot in $M_3$-$CuA_1$ cell (vs. narrow streak or no spot at all).

Using Evans (1952), the new species keys out to *E. gentius*, which was considered the sole species in this group by Evans. The neotype for *E. gentius* was designated by Austin *et al.* (1997), and two other species in the group: *E. bombus* and *E. aureolus*, were described. Austin *et al.* (1997) provided a key to *Entheus* males from their Rondônia study site, which keyed the new species to the choice between *E. aureolus* ("Yellow-orange, tuft on hind tibia with dark tip, VHW anal margin yellow", the holotype Figs. 3–4, 28 part) and *E. bombus* ("Yellow, tuft on hind tibia entirely yellow-orange, VHW anal margin black", the holotype Figs. 7–8, 28 part). The choice is inconsistent, because the new species can be described as "yellow-orange, tuft on hind tibia with dark tip, VHW anal margin black." However, according to Austin *et al.* (1997), this combination of characters refers to *E. gentius* (Figs. 5–6, 28 part), which has not been recorded from Central Rondônia and therefore not included in the key, but is re-described in detail in

**Figures 1–8. (Opposite page) *Entheus gentius* group males. 1–2.** *E. huertasae* **n. sp.** holotype, Colombia: Santander department, Magdalena River Valley, near Barrancabermeja, elevation 100-150 m (location data deduced from the label), genitalia vial No. NVG130531-08 (genitalia shown in Fig. 26); **3–4.** *E. aureolus* holotype; **5–6.** *E. gentius*, Brazil: Pará, Obidos, 1-Aug-1982, leg. Miers, OM 38.416, genitalia prep. Mielke 1994; **7–8.** *E. bombus* holotype. Dorsal and ventral surfaces are shown on odd- and even-numbered figures, respectively. Magnified antennal club of *E. huertasae* holotype with nudum segments count is shown between the images of the specimen. G. W. Lambertz drawing used as a basis for published engraving of *E. gentius* original description by P. Cramer (1777) is shown between the images of the specimen and is copyright (©) Trustees of the Natural History Museum, London (used with permission). Labels are shown for primary types in-line with the specimen images. Labels are reduced 2.5 times compared to specimens: small scale bar below *E. huertasae* locality labels refers to labels, and larger scale bars refer to specimens. **1–2** is in AMNH collection, other specimens are in DZUP collection and are photographed by Ernst Brockmann.


Panama
F
9
10
11
12
E. huertasae
1 cm
13
14
15
16
17
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21
22
23
24

the text. The Austin *et al.* (1997) description of *E. gentius* additionally indicates: "portion in [forewing] discal cell hyaline (this latter appears to be a unique character for *E. gentius*)", dorsal hindwing "with very broad (nearly 1/3 wing width) black outer margin", "anal margin ... black", and "penis robust". The new species does not have hyalinity in the discal cell, its dorsal hindwing margin is much narrower, only slightly broader than that of *E. aureolus*, (Figs. 1–2 & 9–24) and aedeagus is narrow and slender (Figs. 26l, 27a) as in *E. aureolus* (Fig. 27b), and not stout as in *E. gentius* or *E. bombus* (Figs. 27c, d). Therefore, the new species exhibits a mixture of characters specified by Austin *et. al.* (1997) for each of the three named species in the *E. gentius* group and does not fully agree with any of these three species.

A combination of the following characters sets the new species apart from all other *E. gentius* group species, with the first three characters being unique to it: **1)** ventral hindwing broadly black in posterior half, cells $CuA_1$-$CuA_2$ and $CuA_2$-2A are largely black, only with some yellow-orange overscaling basad (and not mostly yellow-orange in the basal half); **2)** three subcostal yellow-orange spots in the subapical band are usually offset basad (along $R_5$), relative to the three submarginal yellow-orange spots; **3)** hindwing anal fold dorsally yellow orange near the base in most specimens (tinted with black and brown in some); **4)** no hyalinity is present in discal cell, the only hyaline spots are the three subapical spots near costa, and not the usual four in other species of the *E. gentius* group; **5)** dorsal hindwing margin is narrowing from apex to tornus, only slightly broader than that in *E. aureolus*, and much narrower than that in the other two species; **6)** outer portion of tibial tuft short (extending distad 1/3 to 1/2 length of first tarsomere), pale brown, darker at the tip; **7)** penis narrow and slender, with long phallobase as in *E. aureolus*, not stout and bulbous as in other two species; **8)** tegumen narrower in lateral view than in other species; **9)** distal processes of tegumen long and slender, almost reach the distal end of uncus, as in *E. gentius* or *E. bombus*, but not shorter and broader as in *E. aureolus*; **10)** uncus longer and less angled than that of *E. aureolus*, dorsally straight with a caudal notch in lateral view; **11)** uncus arms narrow, like those in *E. aureolus*, not as stout as in the other two species; **12)** costal process of valva broadly curved as in *E. aureolus*, less straight than in other two species.

**Variation.** To illustrate variation, all but one paratypes are shown (Figs. 9–24) in addition to the holotype (Figs. 1–2). The contours of yellow orange discal forewing band varies, e. g. the band is strongly constricted along the cubitus in the holotype and some paratypes (e. g. Figs. 1 & 15), but is almost straight along basal edge in others (e. g. Fig. 13). The extent of offset in the apical forewing band is variable: the 3 hyaline spots by the costa may be very strongly offset basad compared to the three yellow orange submarginal spots (e. g. Figs. 1, 11 & 15), or almost aligned, especially along basal edge (Fig. 21). Anal fold dorsally, varies from mostly orange yellow in the majority of specimens, including the holotype (e. g. Figs. 1, 9, & 19) to almost brown (i.e. orange-yellow, overscaled with black-brown), except the very base (Fig. 23). The color of hind tibial tuft varies from paler yellow-brown to darker, almost brown, and the color of the tip could be from brown to almost black, but the tip is always darker than the base (compare Figs. 9–24).

## Discussion and key to males in the *E. gentius* group

The family Hesperiidae offers an astonishingly broad array of possible evolutionary scenarios for the study of relationships between phenotype and genotype and their relevance to speciation. Quite a few species are easy to tell apart both by facies and genitalia, e.g. in genera *Myscelus* Hübner, [1819] and *Aethilla* Hewitson, 1868. A number of genera are well known for similarity in wing patterns, but genitalia are easily diagnostic for their many species, e.g. blue *Elbella* Evans, 1951, *Staphylus* Godman & Salvin, 1896, or *Erynnis* Schrank, 1801. The opposite scenario, when genitalia are alike and species can be more readily told apart by facies, is quite rare, but *Amblyscirtes* Scudder, 1872 comes to mind. This scenario is rare because, by definition, consistent differences in genitalia are typically viewed as an indication for species status (Burns, 2000; Austin & Warren, 2002). Therefore in the absence of notable differences in genitalia, hypothesizing about speciation is more difficult to support.

A fourth possible scenario can take place as well, when both facies and genitalia are similar and do not allow for confident placement of species boundaries. Such a conundrum was best revealed by the consorted analysis of life history data and a short snippet of genotype dubbed "barcode," which is a 654 base pair region of mitochondrial DNA encoding for the C-terminal segment of cytochrome c oxidase subunit I (COI). The best example is the skipper known as *Astraptes fulgerator* (Walch, 1775) which is likely an assembly of many cryptic species that at present cannot be identified with confidence by adult facies nor genitalia, but instead by caterpillar foodplants, patterns and ecology, and for many of them distinct DNA barcodes (Hebert *et al.*, 2004). *Entheus* belongs to the same skipper subfamily as *Astraptes* Hübner, [1819], and the studies of Janzen *et al.* (2011) revealed a similar situation in the "species" formerly identified as *E. matho* in collections. Three distinct *E. matho*-like species very similar in appearance and genitalia are sympatric in northwestern Costa Rica. A number of

**Figures 9–24. (Opposite page) *Entheus huertasae* n. sp. paratypes.** All are from Panama: **9–10** & **13–14**. Panamá Prov.: Distrito de El Llano, Cordillera de San Blas, N. of El Llano, 330 m, 19-May-1978, genitalia vial No. NVG131124-01, DNA NVG-1759 (**9–10**) and 6-Jun-1978 (**13–14**); **11–12**. Darién Prov., Darién National Park, Rancho Frio, 08° 01' 11.3"N 77° 43' 57.0"W, 100 m, 22-Jul-2013; **13–14**. Panamá Prov.: Distrito de El Llano, Cordillera de San Blas, N. of El Llano, 330 m 6-Jun-1978; **15–18** & **21–22**. Panamá Prov.: 5 mi N. El Llano, 9° 17'N 79° 00'W, 330 m, 5-Jun-1978 (**15–16**), 8-Jun-1978 (**17–18**) and 8-Jun-1978 (**21–22**); **19–20**. Panamá Prov., Cerro Jefe, 490 m, 24-Sep-1973; **23–24**. Veraguas Prov., near Punta Mariato, 800 m, 7° 13'N 80° 53'W, 12-Feb-1982. Dorsal and ventral surfaces are shown on odd- and even-numbered figures, respectively. A segment of a photograph with hind leg with tibial tuft is shown between specimen views. "F" indicates mirror image (left-right inverted). All specimens are in USNM collection and are leg. G. B. Small, but the one shown in **11–12**, which is leg. A. Thurman and is in the research collection of A. Thurman.

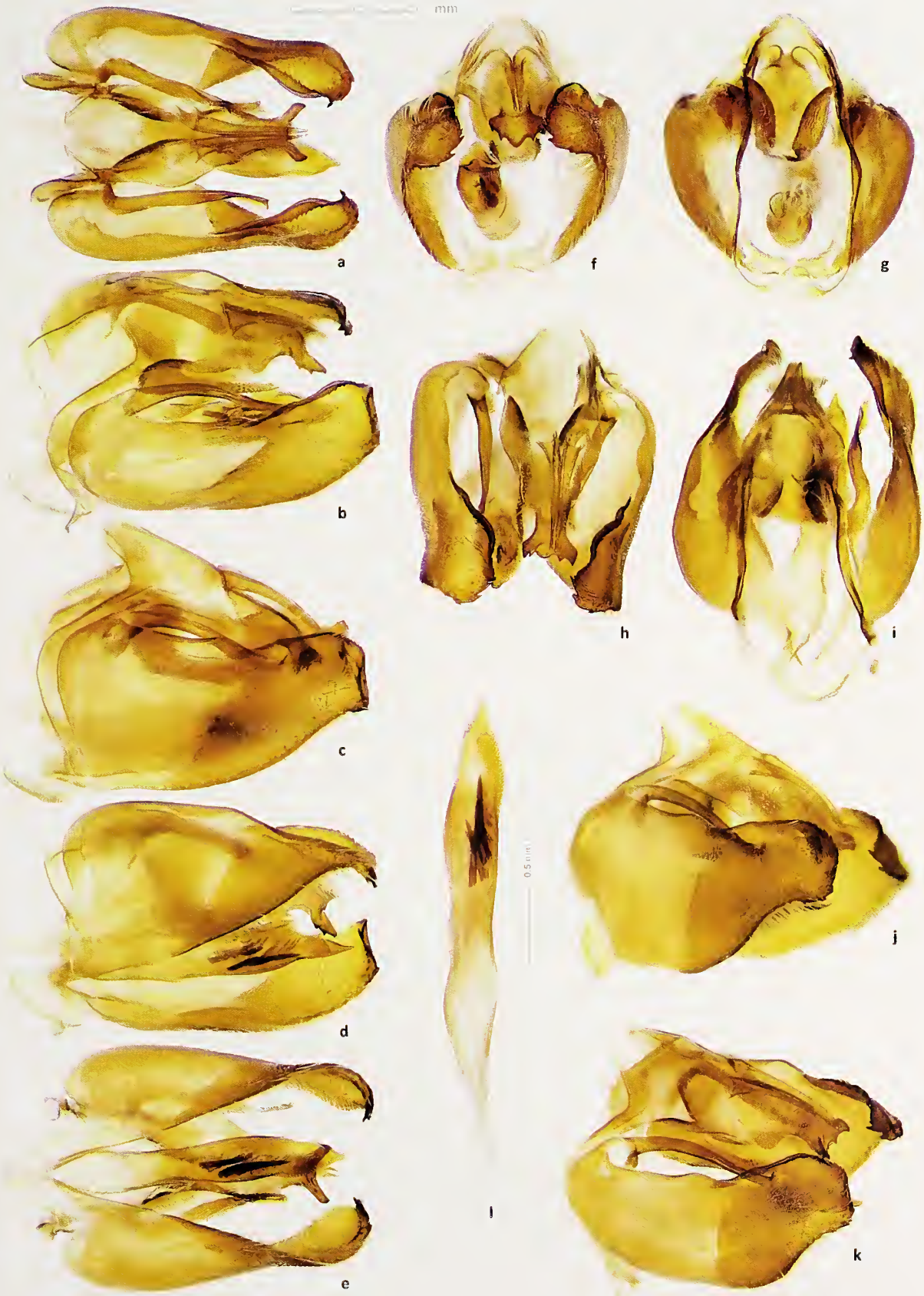
studies report close similarity in *Entheus* genitalia, even for species that are not very close to each other phylogenetically (Steinhauser, 1989; Austin *et al.*, 1997; Austin, 1997; Grishin, 2012). Some of these species are easier told apart by wing patterns than by genitalia (Austin *et al.*, 1997; Grishin, 2012). Thus, *Entheus* might be another example where wing pattern differences are more indicative of speciation than genitalia.

These results indicate the difficulties with *Entheus* taxonomy and evaluation of the status of proposed names. For instance, the three *E. gentius* group species, two of which were named by Austin *et al.* (1997), were all considered to be a variable single species by Evans (1952). On a casual look it is easy to dismiss moderate-at-best differences in wing patterns (Figs. 2-8, 28 part) and subtle differences in genitalia as intraspecific variation and synonymize these recently proposed names under *E. gentius*. However, available DNA barcode data strongly support Austin's *et al.* (1997) treatment (Fig. 29) and confirm that these differences, both in facies and genitalia, are indeed taxonomically meaningful. Despite general similarity in appearance, DNA barcode divergence between *E. aureolus* and *E. gentius* exceeds 7%, and is significantly larger than barcode divergence among the three undescribed Costa Rican species (1.1–2.3%), and almost twice as large as that between *E. priassus* (Linnaeus, 1758) and *E. crux* Steinhauser, 1989 (4%), which belong to different *Entheus* species groups, and were never considered to be very similar. The same refers to the comparison of *E. priassus* and *E. matho dius* Mabille, 1898 (5.2%). While a more detailed interpretation of extreme divergence between cryptically similar *E. aureolus* and *E. gentius* awaits further studies, it suggests that it is best to treat these taxa as distinct biological species. Divergence between *E. gentius* and *E. bombus* placed as sister taxa in the barcode tree in accord with similarity in their facies and genitalia (Fig. 29) is also substantial (4%) and is in agreement with their treatment as distinct species. As expected from morphology, DNA barcode confidently (90% bootstrap) groups *E. huertasae* **n. sp.** with *E. aureolus* (Fig. 29). Strongly supporting distinctness of *E. huertasae* as a species, the barcode difference from *E. aureolus* is quite large: 6.7%, and the difference exceeds 7% between *E. huertasae* and either *E. gentius* or *E. bombus*.


**Figure 25. Map of *E. huertasae* n. sp. localities.** Localities where specimens were collected are marked with black circles. Type locality is labeled "TL".

Such a high divergence in the *E. gentius* group is not likely explained by some errors in the data, because the tree topology (Fig. 29) is entirely consistent with the grouping by wing patterns, although many nodes in the tree lack statistical confidence due to barcode region being very short. For instance, this tree being rooted with the *Hyalothyrus neleus* (Linnaeus, 1758) sequence places *E. eunyas* Austin, Mielke & Steinhauser, 1997, which is a representative of the *E. eumelus* (Cramer, 1777) group, at the base of the tree consistently with the lack of costal processes on the valva and other characters that are likely to be synapomorphic for all other *Entheus* groups except the *E. eumelus* group. Next, all three species from the *E. gentius* group cluster together and are placed as a sister group to the rest of *Entheus* taxa, in accord with the Evans (1952) key arrangement. Finally, all species from the *E. matho* group (all remaining taxa except E. *priassus*) cluster together. Two other curious observations from this preliminary analysis are that *E. crux* is a sister of "Burns01": there is indeed a strong similarity in wing patterns of males, but females are very different (dark-brown hindwing vs. white with brown margin); and barcode of the recently described *E. warreni* is quite different from the rest (about 4%), supporting the proposed species status of this taxon named from a single specimen and confirming its placement in the *E. matho* group in agreement with wing pattern characters.

**Figure 26. (Opposite page) *Entheus huertasae* n. sp. male genitalia, holotype.** Genitalia vial No. NVG130531-08. Genital capsule in different views: **a.** dorsal; **b.** left dorsolateral; **c.** left lateral; **d.** left ventrolateral; **e.** ventral; **f.** posterior; **g.** anterior; **h.** dorsoposterior, slightly tilted to the right; **i.** dorsoanterior, slightly tilted to the left; **j.** left lateroposterior; **k.** left dorsolaterposterior. l. penis in ventral view, digitally removed from the genital capsule and edited. All images are to scale shown on the top, except l, which is magnified and a scale for it is given to the right.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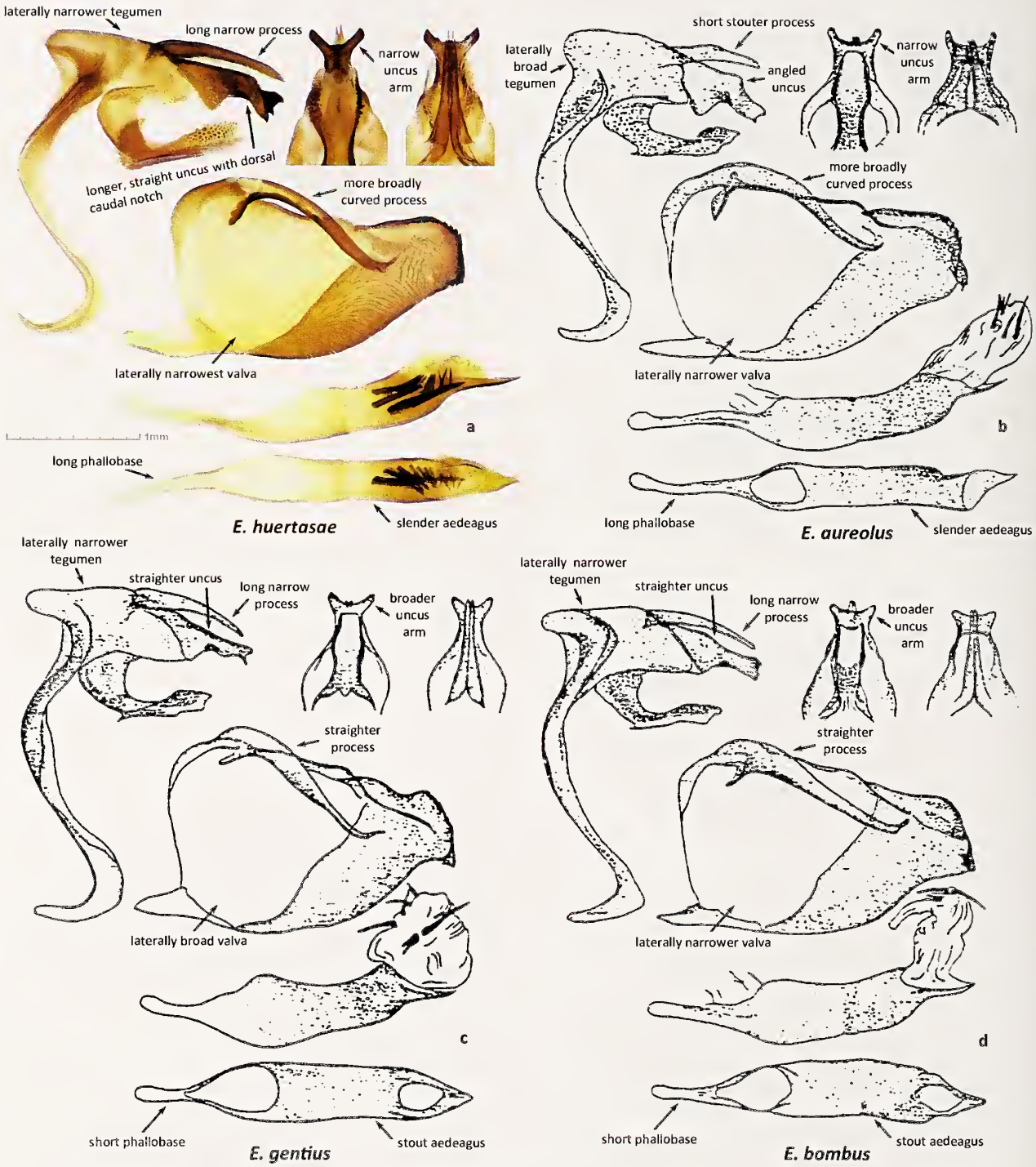


**Figure 27. Male genitalia of species in *E. gentius* group. a**. *E. huertasae* **n. sp.** paratype (genitalia vial NVG131124-01, specimen and data in Figs. 9–10); **b**. *E. aureolus* paratype, Brazil: Rondônia, 3 km E Fazenda Rancho Grande, lot 18, 22-Sep-1992 (GTA #2513); **c**. *E gentius* neotype (GTA # 5766); **d**. *E. bombus* holotype (GTA # 2512). Images show lateral view of tegumen, gnathos, uncus, and associated structures; dorsal (on the right) and ventral (on the left) views of uncus, gnathos, and posterior tegumen; interior view of valva; left lateral (above) and dorsal (below) views of penis (latter without vesica and cornuti on the drawing). "F" indicates mirror image (left-right inverted). The scale refers to photographs (**a**), the drawings (**b–d**) are scaled approximately and are reproduced with modifications from Austin *et al.* (1997), used with permission. Differences between species are indicated on the image.

While the barcode tree in this case is only confirmatory of existing taxonomic work based on traditional specimen analysis, it addresses the concerns about possible over-splitting in *Entheus* on the basis of seemingly minute characters that may not have biological relevance. Indeed, the barcode data suggest that *Entheus* is rich in cryptic species and small, but consistent features of wing patterns might be indicative of speciation. Correlating DNA divergence with phenotype, we can identify the characters that are more likely to be significant for species delineation rather than those that are caused by intraspecific variation. For instance, the width of the hindwing black margin, offsets in the subapical forewing band (revealed in Costa Rican undescribed species), robustness of aedeagus, shape of uncus in lateral view and length and shape of distal processes of the tegumen should be good characters to use. All these characters highlight the differences between *E. huertasae* **n. sp.** and the other three species in the *E. gentius* group.

The following key (see below) is proposed for the males of the *E. gentius* group species. The key is largely based on Evans (1952) and Austin *et al.* (1997), with minor modifications and the addition of *E. huertasae* **n. sp.** to the group. *E. huertasae* is placed first and is immediately distinguished from the rest of the species due to its distinctive appearance and simplicity of recognition by the three unique easy to observe characters: **1)** broadly black ventral hindwing in posterior half, **2)** a triplet of forewing subapical spots offset along vein $R_5$ and **3)** dorsally yellow (at least at the base in most specimens) anal fold. Therefore it will be the species that is the most straightforward to recognize both in dorsal and ventral aspects. However, DNA barcode (90% bootstrap in the NJ distance tree, Fig. 29), genitalia (more slender aedeagus and uncus arms, valva narrower in ventral view, more curved costal process of valva) and narrow hindwing margin of *E. huertasae* are more similar to *E. aureolus* than to the other two species. Therefore it is most likely that *E. huertasae* is a sister to *E. aureolus* rather than being basal to the group. I suggest the following linear order for the species in the *E. gentius* group that is expected to be phylogenetically meaningful: {(*gentius*, *bombus*), (*aureolus*, *huertasae* **n. sp.**)}. The two pairs in parenthesis are likely sister species. The characters that seem the easiest to observe are underlined in the key. Most pattern characters are illustrated in Fig. 28 and genitalia of type specimens compared in Fig. 27.

**Key to the males of the *E. gentius* group species.**

**0.** Hindwing largely yellow or yellow-orange with dark brown or black margin. Forewing spots and bands yellow or yellow-orange, sometimes at least partly hyaline closer to the apex and costa, but not white. Rhomboidal orange-yellow spot in cell $M_3$-$CuA_1$ (not a narrow streak) ..... ***Entheus gentius* group** males

**1a.** Hindwing with a narrowing black margin dorsally near tornus, but ventrally broadly black in the posterior half, i.e. space from $CuA_2$ vein to anal margin almost entirely black and black scales are present in $CuA_1$-$CuA_2$ cell from its base. Hindwing anal fold black ventrally and orange-yellow dorsally at least at the base in most specimens, but may be partly covered with dark scales. In the forewing subapical yellow-orange band, three anterior spots offset basad along vein $R_5$ from the three posterior spots. Forewing discal cell yellow spot without hyaline areas. Tuft on hind tibiae short, mostly pale brown with slightly darker tip. Orange yellow in color. Penis longer, more slender. Processes of tegumen long and narrow, reach the end of uncus. Panama, Colombia (TL: Magdalena Valley) ..... ***E. huertasae*** n. sp.

**1b.** Hindwing in some species may be with broad black margin dorsally, but ventrally largely orange-yellow except the dark marginal band and sometimes anal fold, i.e. cell $CuA_2$-2A yellow orange at least in its basal half and the base of $CuA_1$-$CuA_2$ cell yellow orange. Hindwing anal fold dorsally black or brown and ventrally may be yellow in some species. All six spots by the forewing apex in a smooth curve, or the distal edge of the curve with a weak basal offset of the anterior three spots compared to the three posterior spots; however, the basal edge either smooth, or with a more prominent distal offset of the two posterior spots (i.e. two submarginal spots in $M_1$-$M_2$ and $M_2$-$M_3$) and the spot in $R_5$-$M_1$ aligned with the three anterior spots (in $R_2$-$R_3$, $R_3$-$R_4$, and $R_4$-$R_5$) rather than with the submarginal spots. Forewing discal cell yellow spot may contain hyaline areas ..... **2**

**2a.** Hindwing black margin narrow dorsally, narrowing towards the tornus, anal margin yellow ventrally (only fringes black), no hyaline areas in the forewing discal cell yellow spot. Tuft on hind tibiae short, with dark tip. Redder than other species, from orange yellow to orange in color. Aedeagus longer, more slender. Processes of tegumen shorter, more robust, end around 3/4 of uncus. Colombia, Peru, Venezuela (Amazonas), Brazil (north, TL: Rondônia), the Guianas ..... ***E. aureolus***

**2b.** Hindwing black margin broad, broadening towards the tornus. Anal margin black or with significant black overscaling ventrally. Hyaline areas in the forewing discal cell yellow spot in one of the species. Tuft on hind tibiae longer, entirely orange-yellow, or with dark tip. Aedeagus more stout. Processes of tegumen longer, almost reach the end of uncus ..... **3**

**3a.** Yellow-orange spot in forewing discal cell with at least one hyaline area. Orange scales invade into and partly cover the black margin near dorsal hindwing tornus creating appearance of an orange tooth. Ventral hindwing with broad black or dark brown anal margin. Tuft on hind tibiae long, with dark tip. Orange yellow in color. Peru, Colombia (south), Venezuela (Amazonas), Brazil (north), the Guianas (TL: Suriname) ..... ***P. gentius***

**3b.** Yellow-orange spot in forewing discal cell without hyaline areas. Orange scales do not invade into the black margin near dorsal hindwing tornus, i.e. areas with black scales form close to right angle from the margin to anal fold. Ventral hindwing with fewer black and more yellow-orange scales along anal margin. Tuft on hind tibiae shorter, entirely yellow-orange. Yellower than other species. Peru, Venezuela, Brazil (north, TL: Rondônia), the Guianas ..... ***P. bombus***


**Figure 28. Visual keys to species in the *E. gentius* group.** Dorsal and ventral aspects for each species are shown on the left and right, respectively. Images shown are illustrations, sometimes composed of photographic segments from left and right sides and digitally edited to highlight the wing patterns instead of damage in specimens. Images are set to be approximately the same size. Unedited and to scale photographs of specimens are shown in Figs. **1–8**. Photographs of all specimens, except *E. huertasae* **n. sp.** are by Ernst Brockmann.

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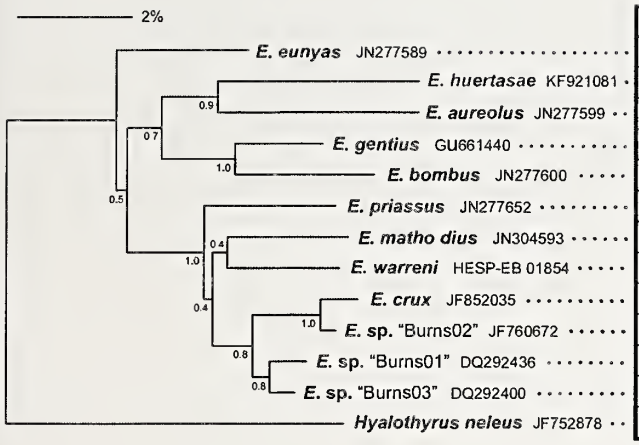
## Editor's note

The electronic edition of this article has been registered in ZooBank to comply with the requirements of the amended International Code of Zoological Nomenclature (ICZN). This registration makes this work available from its electronic edition. ZooBank is the official registry of Zoological Nomenclature according to the ICZN and works with Life Science Identifiers (LSIDs). The LSID for this article is: urn:lsid:zoobank.org:pub:IE937079-C466-4I78-ADI5-4C02F307C986. Registration date: December 26th, 2013. This record can be viewed using any standard web browser by clicking on the LSID above.




| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 654 | 48 | 50 | 35 | 40 | 41 | 34 | 41 | 40 | 38 | 35 | 36 | 61 |
| 2 | 7.4 | 654 | **44** | **47** | **50** | 53 | 54 | 54 | 54 | 54 | 51 | 49 | 77 |
| 3 | 7.7 | **6.7** | 654 | **45** | **47** | 50 | 55 | 49 | 55 | 53 | 53 | 53 | 78 |
| 4 | 5.4 | **7.2** | **6.9** | 654 | **25** | 40 | 45 | 47 | 44 | 42 | 41 | 42 | 69 |
| 5 | 6.2 | **7.8** | **7.3** | **3.9** | 645 | 48 | 50 | 49 | 51 | 49 | 48 | 45 | 71 |
| 6 | 6.3 | 8.1 | 7.6 | 6.1 | 7.4 | 654 | 34 | 28 | 29 | 27 | 27 | 24 | 71 |
| 7 | 5.2 | 8.3 | 8.4 | 6.9 | 7.8 | 5.2 | 654 | 26 | 31 | 29 | 23 | 24 | 69 |
| 8 | 6.3 | 8.3 | 7.5 | 7.2 | 7.6 | 4.3 | 4.0 | 654 | 33 | **31** | 27 | 22 | 70 |
| 9 | 6.1 | 8.3 | 8.4 | 6.7 | 7.9 | 4.4 | 4.7 | 5.0 | 654 | **6** | **18** | **17** | 72 |
| 10 | 5.8 | 8.3 | 8.1 | 6.4 | 7.6 | 4.1 | 4.4 | 4.7 | **0.9** | 654 | **14** | **15** | 68 |
| 11 | 5.4 | 7.8 | 8.1 | 6.3 | 7.4 | 4.1 | 3.5 | 4.1 | **2.8** | **2.1** | 654 | **7** | 66 |
| 12 | 5.5 | 7.5 | 8.1 | 6.4 | 7.0 | 3.7 | 3.7 | 3.4 | **2.6** | **2.3** | **1.1** | 654 | 68 |
| 13 | 9.3 | **11.8** | 11.9 | 10.6 | 11.0 | 10.9 | 10.6 | 10.7 | 11.0 | 10.4 | 10.1 | 10.4 | 654 |

**Figure 29. DNA-derived data.** The mitochondrial DNA COI barcode (654 base pairs) distance matrix is shown on the right and a BioNJ distance tree (Dereeper *et al.*, 2008) corresponding to it is on the left. The 2% difference scale bar is placed above the tree. Bootstrap support values are shown by each node in the tree. Values below 0.6 correspond to less certain and possibly erroneous groupings. GenBank accessions (http://genbank.gov) are indicated to the right of each species name, except that for *E. warreni* sequence, BOLD database (Ratnasingham & Hebert 2007) voucher code is given. The *Entheus* tree was rooted with *Hyalothyrus neleus* (Linnaeus, 1758) sequence. Identification is based on specimen images from the BOLD public web-pages linked to from the "db_xref" fields in the GenBank sequence pages, and should be considered preliminary for some taxa. In the distance matrix, percent difference, the number of different nucleotides and the number of base pairs in a sequence are shown below, above and on the diagonal, respectively. Values corresponding to differences between the four *E. gentius* group species (all specimens from Brazil: Amazonas, except *E. huertasae*, which is from Panama, DNA extraction NVG-1759, full data in text) and four phylogenetically close species in the *E. matho* group are shown in bold. Three of the *E. matho* group species ("Burns01", "Burns02", and "Burns03", sympatric in Costa Rica: Guanacaste Province) remain unnamed, but differences between them have been reported (Janzen *et al.*, 2011).

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